Essentials of Animal Behaviour

Essentials of Animal Behaviour is an introduction to the study of animal behaviour and is primarily intended for first or second year undergraduates attending short courses in the subject. The book concentrates on putting across the basic principles as briefly and lucidly as possible with the aid of carefully selected examples from both the recent and classic literature, together with numerous illustrations. It will enthuse readers with this active and exciting area of research, and will lay a solid foundation on which further study may be based. Its simple and readable style, helped by an extensive glossary, will also make it useful to senior level school students, their teachers and those with a general interest in the subject. It will be particularly rewarding for all those needing the basics in animal behaviour, behavioural ecology and comparative psychology.

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Essentials of Animal Behaviour

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Contents

Preface

The aim of this book is to provide a brief, but reasonably comprehensive, introduction to the study of animal behaviour. It has grown out of my earlier book, *An Introduction to Ethology*, which was published 12 years ago and has been out of print for some time. Twelve years is a long time in an active field of science, and a lot of interesting things have happened during that period, so the book needed a good going over and sprucing up. But fashions change in science, as in all else, so some parts of the book, describing fields that have seen little recent work, are much as they were before, while I have written new sections and modified the text extensively in those areas in which there has been a lot of recent interest. One obvious change is in the title: the word 'ethology' to describe animal behaviour, and 'ethologist' for someone who studies it, while admirably concise, have rather fallen from use. Unfortunately they have tended to be tied in people's minds to the particular school of study and theories that emanated from Europe in the middle years of this century. Many of these theories have not been supported by later work, and the word ethology has tended to sink with them. It probably sank somewhere in the middle of the Atlantic, as it never really made it to the far side anyway!

The theories of the ethologists were clear and simple and provided a magnificent body of hypotheses on which subsequent work could be based. For this reason, the approach I shall take here is a somewhat historical one, looking at the ideas of the early ethologists, notably Konrad Lorenz and Niko Tinbergen, and then surveying developments over the past few decades to identify subsequent work which has been influential in leading to what we now think about animal behaviour. I have tried to choose some of the best examples, from among both classic studies in the field and the great range of recent work, to illustrate my themes as clearly as possible for those with no previous knowledge of the subject. These have the excitement of approaching this fascinating subject for the first time; if I can share some of the thrill I felt when I did so, this book will have succeeded.

I remain grateful to those who read sections of my earlier book. Three referees made very useful comments and suggestions about what to change and what to leave as it was, and the ideas of various colleagues have helped me with parts of the book, while Jeff Graves read the glossary and Vincent Janik made helpful suggestions on the whole text. It is a particular pleasure to thank Nigel Mann for his delightful illustrations, as well as Jan Parr for some that have been carried over from my previous book, and Tracey Sanderson and Jane Bulleid for seeing the book speedily through the presses.

P. J. B. S. St Andrews, 1998

1

Asking questions about behaviour

People have been fascinated by the behaviour of animals for a long time. Their interest was caught both by the eye-catching activities that they could see around them in the natural world and by the need to understand and control the behaviour of their own domestic animals. Questions naturally arose in their minds. Aristotle, for example, wondered where swallows went in the winter and, seeing them gathering in reedbeds, he speculated (as he did about a lot of things!) that they hibernated in the mud at the bottom of ponds.

But the scientific study of behaviour is a recent phenomenon and, as with so much else in biology, it received its most important boost from the writings of Charles Darwin. Darwin included a chapter in *The Origin of Species* on 'Instinct', a term used in his time to refer to the natural behaviour of animals. He also wrote a book specifically about behaviour called *The Expression of the Emotions in Man and in Animals*. Despite this, in the half century after Darwin there was little work on the behaviour of animals, while zoologists grappled with trying to understand the fundamental principles of systematics, physiology and developmental biology. A few scientists from that time, like Julian Huxley in Britain, Oscar Heinroth in Germany and Charles Otis Whitman in America, stand out for their contribution to behaviour, but they were a small band. It was only in the 1930s that a comprehensive theory of animal behaviour began to emerge through the writings of Konrad Lorenz and, later, of Niko Tinbergen. These men founded the European school of ethology, 'the biological study of behaviour' as Tinbergen defined it. In 1972, this field really came of age as a science when Lorenz and Tinbergen received the Nobel Prize for physiology. They shared it with Karl von Frisch, who discovered the remarkable dance of the honey bee, which enables foragers to tell others in their hive the location of good food sources. This prize was recognition indeed that these three men, whom many saw simply as naturalists, had made a fundamental and lasting contribution to science (Figure 1.1).

It is, in fact, excusable to think of the study of animal behaviour as being a branch of natural history, for the diversity of nature has always been a source of interest and wonderment to those who, like ethologists, studied the natural behaviour of animals. Observing and describing exactly what animals do is fascinating in its own right, and it is also an essential prelude to a more scientific analysis of their behaviour, as was stressed by the early ethologists. It pays to know your animal! Thus spending long hours patiently watching animals (Figure 1.2) can, in itself, be quite revealing even if it is not extended to forming hypotheses and carrying out experiments.

As a result of this preliminary period of thorough and careful description one can make an inventory, or ethogram, of the behaviour patterns of the species being studied. To the casual observer it might look as though different species of birds or of fishes behave much the same as each other. It might also seem that the behaviour of each animal is a highly varied business, not easy to split up into particular categories. Fortunately, for most animals, these impressions are not totally true. Each species tends to have an array of stereotyped behaviour patterns, some of which may be shared with related species but others of which are unique to itself. Describing them and recognising them each time they appear is not as difficult as it might at first seem.

1.1 A case history

Let us illustrate this point with an old favourite of behavioural studies, the three-spined stickleback, an especially easy species to study as it behaves more or less normally in an aquarium tank. Male sticklebacks come into breeding condition in the spring when daylength increases and the streams in which they live become warmer. They change colour, becoming bright red on the underside and iridescent blue on the face, and their behaviour also alters. They gather weed and collect it at a particular spot on the bottom of their pond, gluing it together to form a nest with a special movement that extrudes a sticky secretion from their cloaca. If another male approaches, the territory owner will chase him away or, if he persists, threaten him by adopting a head-down posture which shows off the red belly in all its brilliance (Figure 1.3*a*). Signals such as this are known as displays. If a ripe female stickleback appears, her belly swollen with eggs, our territory owner behaves quite differently, showing another display known as the zig-zag dance (Figure 1.3*b*). He darts alternately

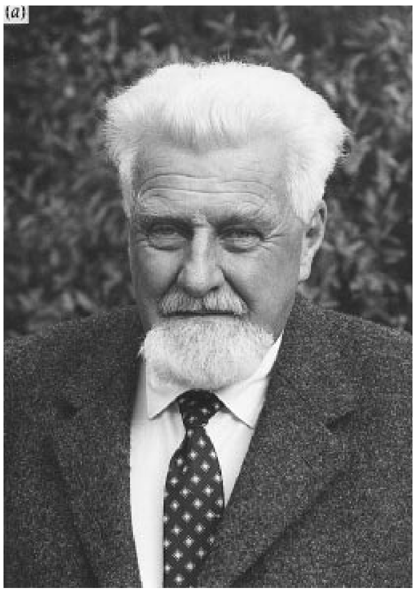


Figure 1.1. Ethology's three Nobel prize winners: Konrad Lorenz, Niko Tinbergen and Karl von Frisch.

Figure 1.2. Though much of the study of animal behaviour today takes place in the controlled environment of the laboratory, the essence of the subject is to understand behaviour as it occurs in nature and, for this reason, much ethological research is still conducted in the wild (photograph © K.J. Stewart).

towards and away from the female in a very striking manner and, if she follows him, he draws her slowly towards his nest. Once there she may creep through the nest and spawn, and he will then follow, fertilising the eggs she has produced as he does so. Her part is then over; indeed he is likely to chase her away, for care of the eggs, and of the young after they hatch, is carried out by the male alone. When he has eggs he stays close by the nest and repairs any damage that it may suffer, as well as showing fanning, a movement that serves to drive a stream of water over the eggs and so keep them supplied with oxygen (Figure 1.3*c*).

This description allows the identification of certain behaviour patterns which are common to all male three-spined sticklebacks in breeding condition: 'gluing', 'head down posture', 'zig-zag dance', 'creeping through', 'fanning'. All these would appear in an ethogram of this species. But the description also raises a great many questions, and it is here that the scientific aspect of ethology begins. Niko Tinbergen recognised that the sorts of questions one could ask about behaviour fell into four different categories: questions about development, about causes, about functions and about evolution. Interest in development might lead one to ask how a male comes to behave in

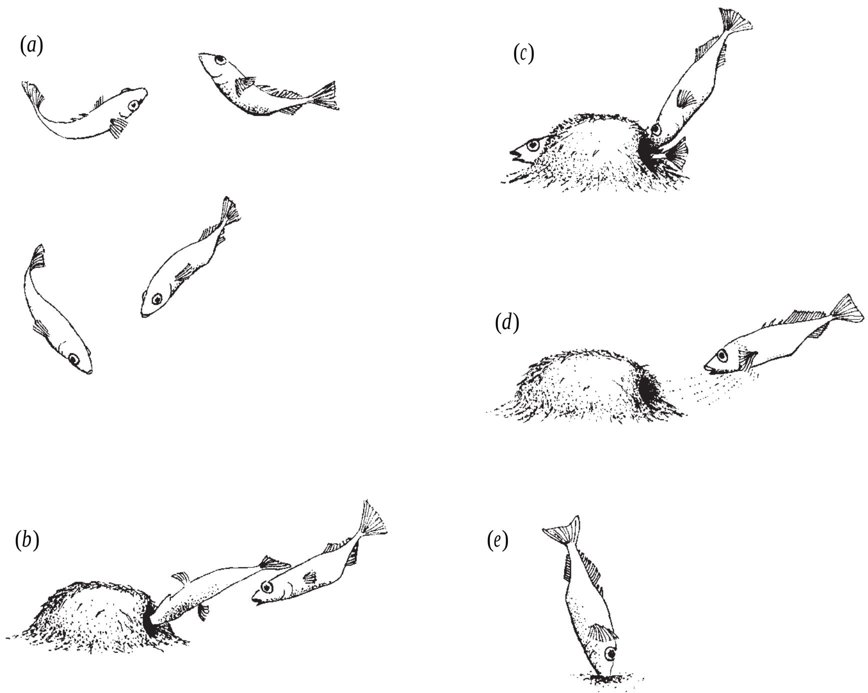


Figure 1.3. Some of the fixed action patterns shown by a male three-spined stickleback in breeding condition. (*a*) The zig-zag dance with which the male leads the female to the nest, at which he shows her the entrance (*b*) and she creeps through and spawns (*c*); (*d*) shows the male fanning at the nest and (*e*) the head-down threat display he shows when another male approaches.

the way that he does during the course of his lifetime. For example, does his skill at nest building improve with practice? Does he court a female the very first time that he sees one or must he learn that this is an appropriate way to behave towards her? On the subject of causes, one asks about the mechanisms underlying behaviour, and this concerns both internal states and external stimuli. What is it that signals the male to come into breeding condition in the spring, and how does this affect his physiology so that he is ready to fight and to court? He behaves differently towards females and towards other males: what difference between them leads him to do so? Functional questions concern the advantages of behaving in a particular way. Why does the male show the zig-zag dance rather than simply swimming to the nest? Does his head down posture actually deter other males from approaching, as it should do if its function is to act as a threat signal? Finally, we can ask about the evolution of behaviour. Comparison between different species of sticklebacks can give us clues about how ancient or recent are particular forms of behaviour. Comparison between displays and other behaviour patterns may suggest what actions formed the originals from which displays have been derived.

This account of the questions with which the study of behaviour is concerned makes it sound as though the subject is a straightforward one attacking well-defined problems and without any great controversy. Such an impression would be totally wrong, however. Scientists interested in behaviour have had to contend with gales blowing from various different directions during their short voyage, as well as with awkward questions from some of their own number determined to rock the boat. This has been no bad thing. The early ethologists, and particularly Konrad Lorenz, put forward sweeping general theories based more on careful observation and brilliant intuition than on thorough experimental evidence. These formed a marvellous source of hypotheses for later research, and as a result of this work more detailed knowledge has accumulated and many of the broad and simple theories have had to be replaced. There has also been a growing reluctance to generalise as it has become clear that different animal species vary a great deal in their behaviour so that all-embracing theories are not likely to be very helpful. Rats are not just large mice, far less small people!

1.2 Development and causation

The first real storm to hit animal behaviour blew across the Atlantic, and came in a confrontation between the ethologists and the American school of comparative psychology. The two groups shared an interest in the behaviour of animals, but they approached it from very different viewpoints. The ethologists worked largely in continental Europe and, being zoologists, they had a respect for evolution and were thus interested in a wide variety of species and the different ways in which they behaved. Despite their name, the comparative psychologists at that stage tended not to be concerned with such comparisons and to study very few species, usually just rats and pigeons, their interest being to look for general laws of behaviour that would hold regardless of the species being studied, and preferably apply to humans as well. Their reputation was for rigorous experimental work in carefully controlled laboratory conditions; most ethologists on the other hand simply observed their subjects behaving freely and they did so in the totally uncontrolled conditions of the animal's natural surroundings, those to which selection had adapted it (Figure 1.4). That two such different approaches to very similar topics should lead to

Figure 1.4. A traditional view of the distinction between ethology and psychology was that the psychologist put his animal in a small enclosure and peered in to see what it was doing, while the ethologist put himself in the box and looked out at what the animals round about were up to. Both approaches have their advantages and this distinction between psychology and ethology is now blurred.

confrontation is not surprising. The battle was fought over the subject of behaviour development, a subject on which the views of the two schools were especially starkly contrasted.

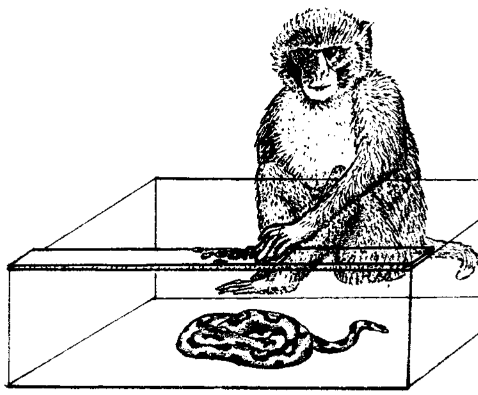
The different views on development of the ethologists and the comparative psychologists stemmed, in essence, from the fact that one stressed nature and the other nurture. To most psychologists the learning ability of animals and the flexibility it gives their behaviour is the main interest in studying them, for these aspects may shed light on the equivalent attributes of humans, hence their stress on nurture. To ethologists, on the other hand, the study of species-typical behaviour was a prime concern: they therefore tended to concentrate on patterns which were highly stereotyped and of similar form throughout a species, and they often referred to such acts as 'innate' or 'instinctive'. The assumption here was that nature was all-important and nurture was of little consequence. Indeed, Konrad Lorenz once remarked that the developmental origins of behaviour was a subject of more interest to embryologists than to ethologists.

This controversy was a bitter one, but it was also fruitful, for each side had much to gain from the other, and its resolution brought them closer together. Psychologists came to recognise that evolution had led animal species to be different from each other and placed constraints on what each could learn. For their part, ethologists came to reject the idea that any behaviour was fixed and inflexible and to realise that the acts they studied, no matter how stereotyped, may have been influenced by learning and by other environmental influences. They also came to appreciate the merits of a carefully controlled experimental approach. Thus today many ethologists work in the laboratory and some of them even use the sorts of equipment developed by psychologists for the study of learning, adapted to shed light on ethological questions. In the battle over nature and nurture, the result has been a synthesis: both sides have gained from the realisation that neither nature nor nurture can be ignored in the development of any behaviour pattern. The borderline between ethology and psychology, once hotly contested, has now broken down and those trained in either field may be found working on a variety of topics of interest to both. A good example of work that spans the interests of both fields is given in Box 1.1.

Box 1.1 Development: fear of snakes in rhesus monkeys

Not surprisingly, wild monkeys are normally frightened of snakes. They have special alarm calls that are given when one is about, and these lead others to be very cautious. They will approach and have a good look, but not get too close. Until the snake has passed the behaviour of the whole troop is altered.

Susan Mineka and her colleagues have studied how young rhesus monkeys in captivity come to recognise snakes and be so afraid of them. They have used a piece of equipment (known, rather pretentiously, as the Wisconsin General Test Apparatus), which is simply a plexiglas chamber into which an object is placed. A hungry monkey is then put on one side of this chamber with food on a shelf on the other, and its fear of the object is assessed by how willing it is to reach across. Wild caught monkeys will not do so when there is a snake in the box, but young ones reared in captivity show no such fear, reaching casually across for the food. If, however, they see another monkey being fearful in that situation, even if only on a video screen, they too will become scared next time they themselves are tested. This suggests that the fear is being passed from one animal to another through social learning. But there is more to it than that, as there is something special about snakes that facilitates the learning. If a videotape is edited, so that the tutor monkey appears to be frightened of a bunch of flowers that has been cut-in in place of the snake that was really there, the observer does not become frightened of flowers. So we have an interplay here between learning from others and a predisposition to learn about snakes.



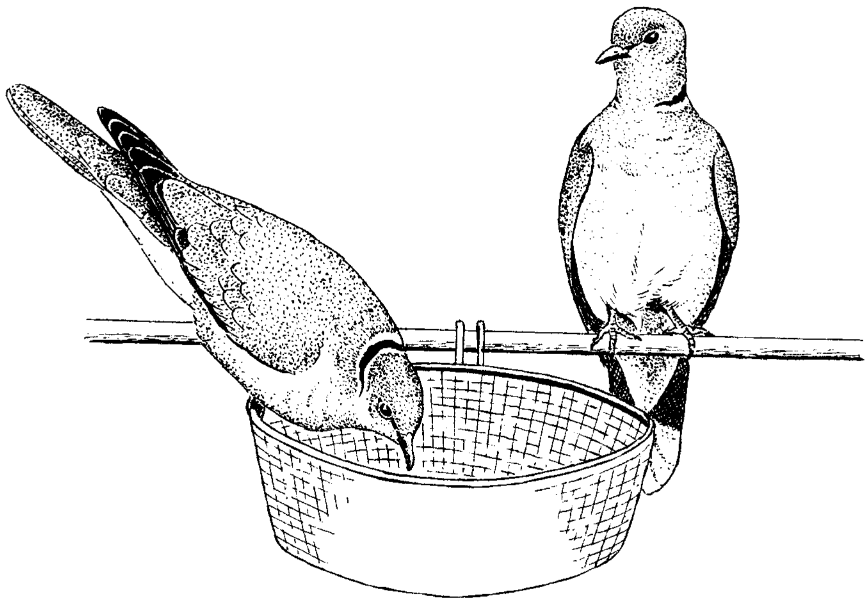
A lot of behaviour development involves such interplays. In this case it is a very neat arrangement. The spectrum of predators in one place may be different from that in another within the range of a species of monkey, and some things that are harmless look very like ones that are not. Learning from the experience of others, but with a bias towards learning to be cautious about some general categories of animal (long thin ones are not a bad start!), is a good developmental strategy, so that the animal comes to avoid things that might harm it but to ignore ones that will not.

Development is just one area that is of interest to both biologists and psychologists studying behaviour. Another is in the field of causation, the study of those outside influences and internal states that lead animals to behave in the way that they do. The senses of animals keep them informed about changes in the external world so that they can react appropriately to many different sorts of stimuli, escaping from those that are potentially dangerous, attempting to capture and eat those that look like food and approaching and courting those that may be prospective mates. Understanding the sensory processes involved is important to shed light on how behaviour is caused, and behavioural studies here border on the interests of the sensory physiologist and the perceptual psychologist. All have the common aim of understanding how events in the outside world are translated into nervous signals and hence into behaviour.

Both physiological psychologists and biologists interested in behaviour may also be interested in how behaviour is influenced by internal events, such as low blood glucose or high levels of a hormone. Just as it is possible to present an animal with a loudspeaker playing a courtship call or a model showing a threat display, so its internal state can be changed: for example, it can be deprived of food so that its blood glucose is lowered or it can be treated with a sex hormone to see whether this affects its behaviour. A full understanding of the causation of behaviour requires knowledge of how both external and internal events affect the nervous system to produce behaviour. Box 1.2 gives an example of a study looking at how these factors interact. To understand causation at all levels also means looking into the exact neural mechanisms involved, the centres and pathways which intervene between senses and movement. This is the realm of the neurobiologist but, from the point of view of understanding the causes of behaviour, it can also be fruitful to treat the animal as a 'black box' rather than probing inside it. For example, one can study the events in the outside world that lead to a behaviour pattern being shown, or how an animal decides which, of the many behaviour patterns in its repertoire, it will carry out at a particular moment. The fact that animals are more willing at some times than at others to show particular responses, like eating, drinking or mating, has led to many different theories of how internal and external factors combine to affect behaviour, collectively known as theories of 'motivation'. Much of the attention of the early ethologists, such as Lorenz and Tinbergen, was devoted to these theories, but recently they have rather fallen from vogue. This is partly because it has become more fashionable to explain the mechanisms underlying behaviour in terms of the animal's neural machinery, as many neurobiologists are trying to do. But it is also because motivation is a very complex matter which requires the taking into account of many different factors for each system of behaviour and cannot be summed up by a simple overall model of the sort that ethologists originally put forward.

Box 1.2 Causation: the incubation of barbary doves

The reproductive behaviour of barbary doves, or ring doves as they are called in the United States, has been studied extensively, particularly initially by Danny Lehrman. If a pair of doves is put together and given a nest and eggs they will not incubate straight away, so the right external stimulus is not all that they need to get the behaviour going. But if a pair has been together for several days, particularly if they have had pine needles with which to build their own nest, they will start to sit when given a nest and eggs even though the female has not laid. Clearly something has happened to change their behaviour.



When the pair are first put together the male starts courting the female, using a display called the 'bowing-coo', with which he struts up and down in front of her cooing (like a dove!). To start with she responds rather little, but after a few days copulation first occurs. At this stage too the male has started carrying nest material to their nest bowl and calling there with another display, the nest-coo. The female follows him to the nest, but leaves when he goes in search of more material. After a day or two, however, she remains behind when he leaves and starts to shape the nest; a further day or two thereafter, when the nest is complete, the first egg appears and they are all set to incubate.

These changes will take place even if the two birds are separated from each other by a wire mesh, so mating itself is not required. But, as far as the female is concerned, the displays of the male are an important factor. Indeed, female doves can be stimulated to lay by the shadow of a male projected onto frosted glass. Interestingly, what these displays appear to do is to encourage the female herself to nest-coo, and this in turn may influence her by self-stimulation. But what leads to incubation? At one level the answer is the stimulation received from displaying and nest building. But what these do is to lead to secretion of hormones. Some of these lead to the production of eggs – obviously also essential for incubation – but the one important for incubation itself is progesterone. If female doves are injected with this hormone before pairing, and given a nest and eggs as soon as they are placed with a male, they will sit at once.

The breeding behaviour of doves is a fine example of how internal factors, such as hormones, and external ones, such as a displaying partner, nest material and eggs, combine to give changes in behaviour. Not only that, but the two birds are nicely synchronised with each other and the changes in behaviour take place at just the right time. Because of their earlier experience, which changed their internal state, the birds are ready to sit as soon as their eggs appear.

1.3 Evolution and function

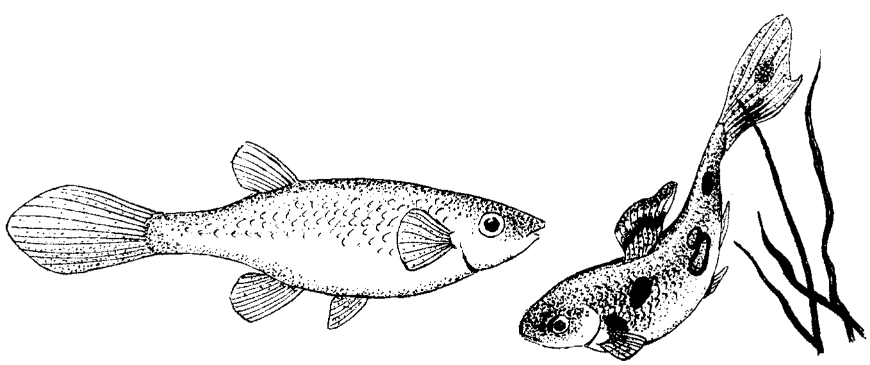
As mentioned earlier, investigating the evolution of behaviour and its function, or adaptive significance, are two other fields of interest, particularly from a biological perspective. In these areas animal behaviour borders on genetics, evolutionary biology and ecology, rather than on topics of interest to psychologists and neurobiologists. The study of behavioural evolution is not an easy task, for behaviour leaves no fossils, so the best that can be done is to reconstruct the course that it must have taken from a comparison of the behaviour of species alive today. Selection experiments and the study of mutants that behave differently from normal animals can also help us to understand the changes in behaviour that must have taken place during the course of evolution. Rarely, as in the case outlined in Box 1.3, evolutionary change can actually be observed taking place.

The major thrust of recent ethological research has, however, been in the field of function: studies aimed at understanding the adaptive significance of behaviour. The last few decades have seen a revolution in our understanding of evolution theory, with the emergence of many stimulating new ideas. Some of these concepts, such as 'inclusive fitness' and 'evolutionarily stable strategies', have particular relevance to behaviour and have led to intensive study, especially of the social behaviour of animals in the wild, in an effort to discover just how natural selection has led their behaviour to be as it is. This field of study, on the border between animal behaviour, ecology and evolution theory, is usually now referred to as behavioural ecology, and has generated some beautiful work. Some aspects of it, especially the subject of sociobiology, which concentrates on putting social behaviour in an evolutionary framework, have also led to a great deal of controversy, much of it rather fruitless. One area of argument has been over the relevance of these ideas to humans, as some sociobiologists (often now calling themselves evolutionary psychologists, just to confuse!) are enthusiastic about the application of evolutionary ideas to humans, believing that our behaviour can be best understood if viewed in the context of our evolutionary heritage.

BOX 1.3 Evolution: the behaviour of guppies in Trinidad

Guppies are small fish that occur in the streams and rivers of northeastern South America and a few Caribbean islands, and they are also common aquarium fish as they are easily kept and bred in captivity. The males have attractive iridescent patches of various colours with which they display to the females. They have been studied particularly in Trinidad by a succession of people, most recently Anne Houde and John Endler, and Anne Magurran and Ben Seghers together with various collaborators. In Trinidad guppies occur in numerous rivers, though obstacles such as waterfalls have sometimes halted their spread. Their morphology and behaviour varies between the different rivers and this has caused particular interest: it provides a rare opportunity to study evolution in action.

A critical factor turns out to be the distribution of predators between the rivers. Some sites are 'high risk' with a range of predatory fish, such as pike-cichlids, while



others are 'low risk' with rather few of them. At the high risk sites males are less brightly coloured and there is some evidence that the females in these areas may prefer them that way, unlike their usual preference for the brightest. In places where a predatory shrimp is common, females prefer males with orange colouration; orange is a colour the shrimp cannot see.

When it comes to behaviour, fish in the high risk sites spend much more of their time in schools, and they are more tightly grouped within these. They are also more cautious when a predator is present, keeping a greater distance from it than fish from low risk areas. That such differences have a genetic basis has been confirmed by the fact that the differences in schooling behaviour persist after several generations of breeding in captivity. Further evidence comes from an experiment where 200 guppies were moved from a high risk area to a virtually predator-free one, above a waterfall where there were previously no guppies. Captive breeding from this population 34 years later showed that their offspring schooled less and were not as wary of potential predators as their ancestors at the high risk sites. Schooling has costs, such as increased competition for food, so that selection might be expected to lead to a decrease in the absence of predators. It is striking that such a decrease could be found after only 100 generations or so.

Guppies breed rapidly and have a short generation time. Not many other species give us opportunities to observe evolution actually happening in the wild. However, as we will see in Chapter 6, comparisons between species can often allow us to reconstruct the sorts of changes that must have taken place during their evolution.

Another, related, bone of contention has been whether or not the claim that behaviour is adaptive means that it is unmodifiable and under tight genetic control: some sociobiologists have written as if it did mean this, and have hence been charged with 'genetic determinism', an especially heinous crime if they are also writing about humans! But, in truth, all that is required for behaviour to be acted on by natural selection is that it has some genetic basis, no matter how slight. There is no reason why its development should be in any sense tightly controlled, so adaptation does not presuppose genetic determinism. And, in the case of humans, behaviour may come to be adaptive for a great many reasons other than through natural selection, notably through our remarkable ability to learn by our own experience and from the experience of others. Indeed, for many of us the environment we occupy is so odd compared with that in which we evolved that it would be hard to argue that our adaptation to it had much to do with selection! Yet we have both modified our environment to suit ourselves and adapted ourselves to it in a fine degree of detail.

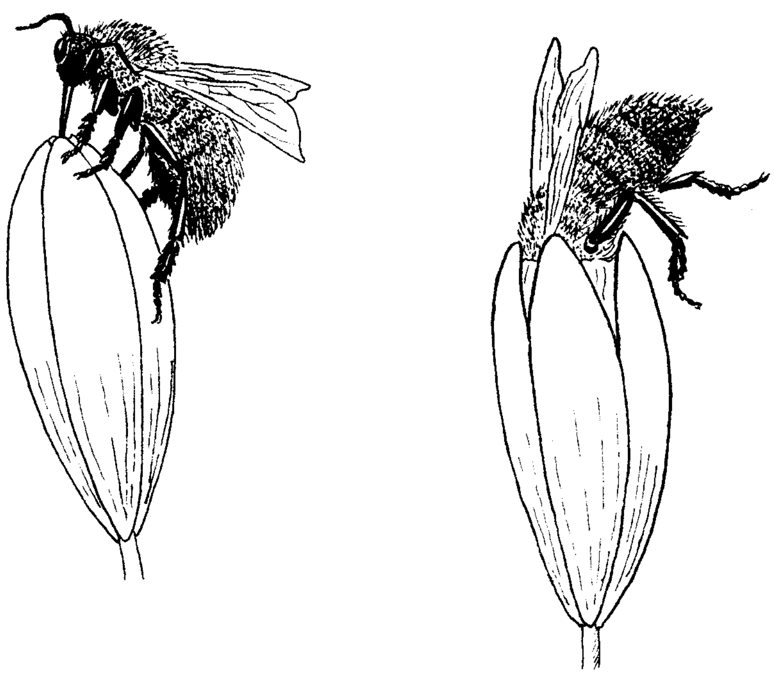
These controversies have generated a good deal of heat, and there are still those who are fiercely committed to one side or the other without a hint of compromise. But reason, as so often, takes a middle course, and neither extreme position is very plausible. Both evolutionary heritage and the genes which are its legacy from one generation to the next clearly influence all the behaviour of all animals, ourselves included, but to argue that either is all-important is as mistaken as to deny that either has any importance. A more serious difficulty with functional reasoning, as with much evolutionary thought, is the ease with which hypotheses can be generated but the difficulty of subjecting them to any rigorous test. Writing popular books, packed with brilliant hypotheses dressed up as facts about the relevance of animal behaviour to humans, is quite a money spinner. Many of the 'just so stories' with which these are filled are so compelling that one feels they just *must* be true – until someone else comes up with an even neater explanation!

The problem is that functional questions are not often easy to test experimentally. To carry out an experiment what one needs is two groups of animals, an experimental and a control, which differ only in that aspect of their behaviour one wants to study. It is not easy to achieve such a very specific change, leaving all other aspects of behaviour the same. Furthermore, adaptation is only relevant to the particular environment in which the species evolved, so the study is most likely to be useful if it is carried out in nature, which further limits the sorts of experiments that can be done. Faced with such problems, many behavioural ecologists have rejected experimentation and concentrated on observation and correlation instead. The results of this can be persuasive, particularly, as in the example shown in Box 1.4, where they are geared to testing specific hypotheses, in this case that bumblebees forage in the most efficient possible manner.

But a correlational approach has problems of its own. The size of monkey troops may correlate with the size of their home ranges, but this fact does not, in itself, provide an explanation. A larger group may require a larger range to feed on, a larger range may require a larger group to defend it, or both features may be caused by a third factor and not directly related to each other at all. For instance, a food supply which is briefly abundant in a small area, then dies out and 'blossoms' once more some distance away, may lead to both. It may encourage a large home range so that there is always at least one source of food present in it. Furthermore, as each source in turn is abundant, group size can be large without disadvantage to the members of the group. Thus large group and large range will both arise without one causing the other. The moral is that one must be cautious about interpreting correlations and that, in function as in other aspects of behaviour, greater certainty can be reached if it is possible to carry out experiments. This is not easy but, with ingenuity, some clever tests of functional hypotheses have been devised.

BOX 1.4 Function: the foraging behaviour of bumblebees

The relationship between flowers and the insects that pollinate them is a close and fascinating one. Insects fly from flower to flower feeding on the nectar that is produced for them as a reward for carrying pollen from one flower to the next. But this is only of benefit to the flower if the insect takes the pollen to one of its own species, for pollen is the plant's equivalent of sperm and is wasted unless it fertilises an egg of the same species. Insects, however, do tend to specialise on the flowers of one species because skills are usually necessary to reach the nectar and, having developed these, they are better equipped to do so. Indeed flower species probably differ from each other in shape very substantially for this very reason: only insects that have developed the appropriate skills can feed on them, and this forces the individual insect to stick to the same species and thus carry pollen from one plant to another of the same sort.



Bumblebees are no exception to this rule, and the adaptiveness of their behaviour has been shown beautifully by Bernd Heinrich. Each bee specialises on one particular flower, referred to as its 'major', while taking occasional nectar meals from other species, its 'minors'. Worker bumblebees are short lived and tend to stick to the same major, but queens live longer and may switch from one to another. Having minors probably enables them to check up on whether another flower has become more profitable than their current favourite. As flowering seasons are short, the abundance of different sorts of flower changes through the year and thus bees are well advised to check that their major still gives the best returns.

Whether it is worth a bee feeding on a particular flower species depends on several factors. Some flowers are much more common than others, so there is little flying time between one meal and the next. Some flowers also produce much more nectar than others so that the meals they provide are larger. Finally, the profitability of a type of flower depends on how many bees are feeding on it. If lots are doing so, then a bee looking for a food source will find that flower rather unprofitable, for there will be little nectar available on each visit. As a result, it is only common flowers with a high rate of nectar production that have large numbers of bees feeding on them. Each bee arrives shortly after another one and so receives little reward, but then it does not have to fly far to the next meal. On the other hand, few bees specialise on rare flowers with a low nectar yield and so each of them gets a large meal at each visit, though it has to fly a long way between one flower and the next to get this reward. Taking all these points into account, Heinrich argued that every bee does about as well as every other in terms of nectar intake per unit time. It follows that it would not pay any of them to switch to a different flower from the one they are majoring on except if these change in frequency. Their behaviour is thus beautifully adaptive to themselves, as well as to the flowers.

1.4 Keeping things simple

One nice thing about animal behaviour as a field is that it is relatively free of jargon compared with many other branches of biology. A glance at the glossary at the end of this book will yield few words that are totally unfamiliar. But there is a hidden problem here, for many of these words are used in a special sense that is not the same as their everyday meaning, and is usually more precise and more restricted. The word function is a good example here. While it is in the vocabulary of most people, rather few mean selective advantage when they say it! There has also been a recent tendency to adopt words from everyday language, which are not entirely appropriate when applied to animal behaviour. Male animals may often mate with unwilling females, and for a while the word rape was used to describe this. But that word carries with it a good many overtones, for example of culpability, which one would not want to apply in animal examples. To refer to 'enforced copulation' may be more cumbersome, but it is also safer. The same argument could be applied to words like 'lying' and 'cheating', though these are now firmly in the behavioural vocabulary. It is important to realise that these words do not imply any malice or evil intention on the part of animals, or indeed that they are thinking anything out for themselves at all. A bird may avoid eating a brightly coloured butterfly that tastes nice because its colour pattern mimics that of another species that tastes nasty. The bird is certainly deceived, but to label such a beautiful adaptation as 'lying' on the part of the butterfly is really going too far!

Problems in the use of words like these are part of the more general issue of 'anthropomorphism', looking at animals as if they were people. The way in which they behave often looks extraordinarily clever and sophisticated, as if they had thought about the problem and decided what the best thing to do was. But beware! Millions of years of evolution can come up with an answer, often in very simple animals with small nervous systems, based on a few rules, which looks not dissimilar to the solution to the same problem we might work out for ourselves. Animals may indeed think things out, have intentions, and behave in all sorts of other ways like we do, but these are very difficult ideas to test scientifically. One of the most important rules in science is that known as 'Occam's razor' which states, in essence, that one should test the simplest hypothesis first and only if it is found wanting move on to more complex ones which are less easy to disprove. Fortunately, as we shall see, some delightfully simple ideas have proved adequate to account for many aspects of the behaviour of animals.

Related to the assumption that animals have intentions is to write as if natural selection had. This is the problem of 'teleology': the implication that there is purpose or design in nature. Natural selection does not act 'in order to' achieve something, but works in retrospect, successful traits persisting and unsuccessful ones dying out. It is a common shorthand among biologists, nevertheless, to write as if selection had purpose; as with the actions of animals, it is best not to for fear of misunderstanding.

Having come up with these strictures, I had better try to abide by them myself without resorting to contorted sentences and leaden prose!

1.5 Book plan

The study of animal behaviour concentrates on four different types of question: causation, development, evolution and function. These topics will form the core of this book and are dealt with, each in turn, in Chapters 4–7. But, as the best studies have always started with a period of description, we will follow this tradition in the next two chapters by describing the motor patterns of animals, their form and what is known of their control, then the senses which give the animal its outlook onto its environment, and how stimuli influence these to produce behaviour. Much of the book will be concerned with individual animals, but we will often refer to their interactions with one another, as when they fight or they mate. In the last two chapters of the book we will come to the social aspects of behaviour more specifically, to discuss communication and the social organisations which are built up by the communicative interactions between individual animals. At the end of the book there is a glossary. This deals with words and phrases in common use among those studying behaviour. Most of these will be found elsewhere in the book, and referring to the glossary may help to remind the reader of their meaning, but I have included others as well in the hope that this dictionary will help the reader who takes the subject on through wider reading. The literature list at the end of the book will, I hope, also help in this. It is not intended to be exhaustive, but gives a list of books in which the reader will be able to take the topics of each chapter to greater depth, and journals where it is worth looking for the latest findings.